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STUDIES ON VERTICILLIUM WILT OF POTATOES¹G. W. AYERS^{2, 3}

Potato 'wilt' has been reported in Prince Edward Island fields since the inception of the seed potato inspection service in 1916. An extensive study of this malady over the period 1937-1939 revealed that practically all wilt was caused by infection of the fungus *Verticillium albo-atrum* Reinke & Berth. During the early years of inspection, the disease was largely confined to the Irish Cobbler variety. Economic losses became greater in later years because of the increased planting of such susceptible varieties as Bliss Triumph, Chippewa, and Sebago. Verticillium wilt is either seed or soil-borne and healthy stock may contract the disease through contact with infected material or contaminated sacks or baskets. Short rotations tend to increase the incidence of the disease. The fungus invades the plant through the roots and may spread from there, through the stem to the leaves. It may gain access to the tubers through the stolons, and some transmission of the disease occurs in this way. In Prince Edward Island and other areas where Verticillium wilt constitutes an economic problem in the production of potatoes, it is important that new varieties should be tested for their reaction to this disease, prior to their adoption commercially, for it is quite conceivable that an otherwise desirable variety may be extremely susceptible to this disease.

The primary purpose of this paper is to present the results of trials for varietal resistance conducted at the Charlottetown Laboratory during the period 1949-1951. Data on the effectiveness of seed treatment are only given insofar as they relate to the study of varietal reaction to the disease. It was found necessary in this study to adopt some means of reducing if not eliminating surface seed-borne inoculum in order to ascertain the extent of transmission by means of internal inoculum.

SEED TREATMENT

Experiments conducted in 1948 and 1949 indicated that treatment with an organic mercurial of tubers from wilted plants is effective in reducing the incidence of the disease. Tubers grown commercially in 1947, were planted in 1948. The plots planted with untreated tubers produced 51.5 per cent and those planted with treated tubers produced 7.1 per cent wilted plants, a highly significant reduction. The experiment was repeated in 1949, the seed used being from the 1948 untreated plots. The percentage of wilted plants was 79.9 from the untreated tubers and 40.2 from the treated tubers, a difference which was also quite significant. It is thought that the poorer control obtained in 1949 was caused by a more extensive invasion of the tubers by the fungus from tubers harvested in 1948 than from those harvested in 1947. Such internally

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borne mycelium would be largely or entirely unaffected by the treatment.

In an experiment conducted in 1950, healthy sets were surface-contaminated artificially with *Verticillium* inoculum. Subsequent treatment of a portion of the sets with an organic mercurial resulted in a high measure of wilt control, whereas severe wilt resulted in the plants from the untreated sets.

VARIETAL RESISTANCE

Materials and Methods

Tubers for the initial phases of the experiment were secured from disease-free sources, and all of the varieties had been propagated and rogued during the year previous to their inclusion in the trials. Some common varieties, which have been grown commercially for many years, were included, as they served as a means of assessing the comparative resistance of new blight and scab-resistant seedlings developed at the potato breeding station in Fredericton, New Brunswick.

The resistance was tested by planting healthy tubers in soil contaminated during the previous year by the planting of infected tubers. The tubers from wilted plants of the various varieties and seedlings were retained for planting during the following year in uncontaminated soil. All of the tubers originating from diseased plants were treated with an organic mercurial in order to eliminate surface-borne inoculum, thereby making it possible to determine whether these varieties were subject to invasion of the tubers by the fungus.

For the purpose of clarity the tests are presented in Series A, B, and C. Each series represents a planting in contaminated soil followed in the ensuing year by a planting of treated tubers from wilted plants in uncontaminated soil.

Series A

The initial trials of 1949 included only five varieties planted in contaminated soil in replicates of six for each variety and with 125 plants in each replicate. In the second phase of this series, seed from wilted plants was planted in 1950 in replicates of six with 60 plants in each replicate.

Series B

Fourteen varieties were planted in contaminated soil in 1950 in replicates of four, with 80 plants in each replicate. The tubers from the wilted plants were planted in 1951 and consisted of four replicates with 40 plants in each replicate.

Series C

Twenty-five varieties were exposed to *Verticillium* soil borne inoculum in 1951, and as in 1950, the plots were replicated four times with 80 plants in each replicate. The presence or absence of seed transmission by the tubers will be determined during the growing season of 1952.

RESULTS

Series A

The four commercially grown varieties Sebago, Irish Cobbler, Green

Mountain, and Katahdin all showed susceptibility to *Verticillium* wilt on exposure to soil-borne inoculum in the tests conducted in 1949. Under similar conditions, Houma contracted negligible amounts of wilt. The plantings in 1950 of tubers from wilted plants of each variety indicated that only the varieties Sebago and Irish Cobbler were capable of transmitting the disease in large amounts by means of internal tuber inoculum. Results obtained in 1950 are quoted from memory as all the data were destroyed by fire.

Series B

As in 1949, the four commercial varieties mentioned above were susceptible to soil-borne inoculum and, again, the Irish Cobbler and Sebago varieties proved to be the important ones for the dissemination of the disease by means of the fungus within the tubers. Houma proved to be moderately resistant to wilt infection and little or no dissemination of the disease occurred by means of fungus elements within the tubers.

The initial results obtained with nine varieties and seedlings, first included in the tests in 1950, showed that all of them are susceptible to soil-borne inoculum, with F458 and Canso more susceptible than the other varieties tested. Seedling F426 exhibited marked ability to develop the disease from the fungus within the tubers; seedling F458, Chippewa, and Canso possessed this character to a lesser extent; and the remaining varieties and seedlings to only a slight extent, with seedling F396 showing the greatest freedom from this type of infection.

Series C

Twenty-five varieties were exposed to soil-borne inoculum in 1951 including eleven varieties and seedlings not tested previously. With the exception of seedlings F4328, F396 and the variety Houma all showed moderate to high susceptibility. Seedling F4328 apparently possesses almost complete resistance, even greater than that found in Houma. The varieties found highly susceptible to soil infestation include Sebago, F458, Canso, F4519, F4514, Kennebec, F1446-26, F469, and Pontiac. The degree of wilt transmission through the seed tubers will be determined in 1952.

FUNGUS ISOLATIONS FROM TUBERS

In September 1951, ten tubers each of ten varieties were selected at random from wilted hills for the isolation of the fungi within them. All of the tubers were surface sterilized and three sections from the stem end of each tuber were plated on potato-dextrose agar. The fungus responsible for the wilt was recovered to a greater or lesser extent from all the tubers. The limited scope of this test permits the mention of only the upper and lower extremes of tuber penetration by the wilt fungus. The *Verticillium* mycelium was recovered from 8 out of 10 tubers of the variety Kennebec, with 70 per cent of all sections containing the fungus.

A successful isolation was obtained from only one tuber of seedling F451, and this single colony represented a recovery percentage of 3.3 for all of the sections plated.

Varietal resistance of potatoes to Verticillium wilt

Variety	Total Plants in Test				Average Percentage Wilt					
	Series A		Series B		Series C		Series A		Series B	
	1949 ¹	1950 ²	1950 ¹	1951 ²	1951 ¹	1952 ²	1949 ¹	1950 ²	1950 ¹	1951 ²
Shelgo	750	360	320	160	320		22.8	mod.	30-40	32.4
Irish Cobbler	"	"	"	"	"		32.1	mod.	30-40	31.8
Green Mountain	"	"	"	"	"		13.5	slight	30-40	4.7
Katahdin	"	"	"	"	"		21.3	slight	30-40	2.9
Houma	"	"	"	"	"		0.8	slight	10-15	1.9
F458	"	"	"	"	"				80-90	19.7
Canoe	"	"	"	"	"				60-70	12.4
F396	"	"	"	"	"				30-40	0.6
F426	"	"	"	"	"				30-40	37.6
F451	"	"	"	"	"				30-40	4.7
Keswick	"	"	"	"	"				30-40	5.1
F393	"	"	"	"	"				30-40	8.9
F384	"	"	"	"	"				30-40	33.2
Chippewa	"	"	"	"	"				30-40	22.3
F4519	"	"	"	"	"					33.3
F4514	"	"	"	"	"					68.0
Kennebec	"	"	"	"	"					65.2
F1446-26	"	"	"	"	"					64.4
F469	"	"	"	"	"					63.9
Pontiac	"	"	"	"	"					62.3
F461	"	"	"	"	"					58.6
F4419	"	"	"	"	"					43.4
F422	"	"	"	"	"					39.4
F424	"	"	"	"	"					29.5
F4328	"	"	"	"	"					24.7
Irish Cobbler				160 ³						1.3 ³

¹Healthy seed planted in *Verticillium*-contaminated soil.²Treated seed from wilted plants of the previous year.³Healthy check.

DISCUSSION

All of the potato varieties and seedlings tested, with the exception of the variety Houma and seedling F4328, have shown moderate to high susceptibility to *Verticillium* wilt on exposure to soil-borne inoculum. Among the susceptible varieties, a marked variation is evident in the extent to which the causal fungus is carried as mycelium in the tubers from wilted plants, and no direct correlation has been found between the extent of the disease when exposed to soil-borne inoculum and the extent to which the fungus is carried in the tubers. These responses by varieties may be classified as follows: (1) varieties showing true plant resistance, as in Houma; (2) those showing susceptibility to soil-borne inoculum but which disseminate the disease but slightly by means of mycelium in the tubers, such as Green Mountain, Katahdin, Keswick; (3) and those varieties showing susceptibility to soil-borne inoculum and which disseminate the disease readily by means of mycelium in the tubers, such as Irish Cobbler, Sebago, Chippewa.

It is significant that economic losses in commercial stands have been confined almost entirely to those varieties falling into the final class.

Verticillium wilt is developed by means of soil-borne inoculum, surface-borne spores, and by mycelium within the tubers. In Prince Edward Island soil-borne inoculum is not believed to cause serious epidemics in the field because of the adoption of long rotations, but it can be an important source of initial infection of potato stock, after which the disease may be perpetuated year after year in the absence of reinfection from soil-borne inoculum. It is probable that the capacity of the fungus to penetrate the tubers is an important factor in the initial establishment of the disease. Subsequent rapid increases in field infection are considered to be dependent mainly on the inoculum present on the seed piece surfaces.

From a study of the records of varieties grown under commercial production for a number of years and from a review of the results recorded in this paper, it would appear that the economic importance of susceptibility to *Verticillium* wilt is dependent on the combined effects of the ease with which infection occurs when exposed to the fungus and the ready invasion of the tubers by the fungus mycelium.

SUMMARY

High resistance to *Verticillium* wilt has been recorded in seedling F4328 and the variety Houma. All other varieties under test have shown moderate to high susceptibility to soil-borne inoculum.

No direct correlation is apparent between the amount of disease developed from soil-borne inoculum and the extent to which the disease is perpetuated by the invasion of the tubers by the fungus.

Susceptible varieties which are capable of readily disseminating the disease by means of mycelium in the tubers include: Irish Cobbler, Sebago, Chippewa, F458 and F426. Economic losses in commercial stands of potatoes grown in Prince Edward Island have been confined to the varieties represented by this class.

METHODS OF OBTAINING SEED ON RUSSET BURBANK AND SIMILAR-FLOWERING VARIETIES OF POTATOES¹JOHN G. McLEAN² AND F. J. STEVENSEN³

INTRODUCTION

The Russet Burbank variety of potato (*Solanum tuberosum* L.) has found little use as a parent because of its male sterility and the early abscission of the blossoms. The methods described herein make it readily possible to use this variety and varieties with similar flower behavior as female parents in potato breeding.

During the 1950 growing season, tubers were selected from Russet Burbank plants which retained unfertilized seed balls in the field. After considerable selection of such plants, it was discovered that the seed balls were retained following underground infection by *Rhizoctonia solani* Kuhn, which frequently resulted in girdling of the stem.

METHODS AND RESULTS

In an effort to simulate the girdling of the stem caused by *Rhizoctonia*, 5 methods of constriction were tried in the field. Each method was tested on the underground stem and at 3 locations on the above-ground stem: at the ground line, half-way up the plant, and just below the blossom. A paired control plant was used with each of the 5 test plants in each treatment. Three flower clusters of each treatment were pollinated with Menominee as the male parent.

Constriction of the Stem—The following methods were used in the field:

1. Stem cut longitudinally half-way through, 2 inches down stem.
2. Stem cut transversely half-way through, 3 sides of plant, 2 inches apart.
3. Cortex of stem removed by scraping 2 inches of stem.
4. Stem constricted by string.
5. Stem constricted by soft wire.

The five methods used constricted all plants. Considerable breakage occurred where the stems had been mutilated by cutting. The removal of the cortex either above or below ground proved to be satisfactory but the growth of the plant was seriously retarded. Difficulties were encountered in the use of string, since the plants were readily cut off when the string was tightened.

The use of soft copper wire (20-gauge) proved to be the most acceptable method. A satisfactory constriction could be obtained by

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tightening 2 strands of wire around the plant (Figure 1A) with pliers until juice could be felt on the far side of the stem. This method proved to be quite rapid without seriously damaging the stem and allowed some further growth of the plant. Girdling just below the clusters was not satisfactory, but constricting the stem 4 or more leaves below the clusters caused the blossoms and seed balls to adhere by preventing the early formation of the abscission layer. Flower retention was better when the plant was girdled before any petals were showing.

The portion of the plants above the point of constriction showed varying symptoms similar to those of *Rhizoctonia* stem damage and corresponding to the severity of the constriction. The symptoms ranged from a dark green, flaccid appearance of the plant to stiffness and upward rolling of the leaves, with yellow and red pigmentation. Few seeds were formed because of the hot weather, but the seed balls were retained on most of the treated plants.

Use of the wire girdle on the breeding plants in the greenhouse proved to be a satisfactory method of obtaining seed on the Russet Burbank (Figure 1B). The girdle was applied beneath the fourth or the fifth leaf below the flowers when the flower stalk was one-half to one inch long and the buds were quite small.

Pollinations were made when the petals were showing, just previous to the opening of the flower. Growth-regulating chemicals⁴ were applied to the pedicel after pollination to impede further the formation of the abscission layer. By using this method it was possible to get crosses on Russet Burbank, Iduna, and B137-5. The flowers on these varieties were readily lost by early abscission if the plants were not girdled.

Growing Flowers and Seed Balls in Nutrient Solution—The application of the wire girdle was not always uniform. There were no girdling effects if the wires were too loose and the cutting of the stem resulted only when applied too tightly. Several stems were accidentally broken at the point of constriction after pollinations had been made. When the broken stems were placed in tap water, the flowers and seed balls continued to grow and eventually produced seed.

To test the use of nutrient solutions for growing potato flowers and seed balls, stems were taken from plants of Russet Burbank, Sequoia, Saranac, and B2102-11 which had been given supplemental feedings of nitrogen, iron, and manganese and were actively growing. Flower clusters were selected which showed different stages of development, ranging from several open blossoms to very young buds on peduncles one-half inch long. The stems were recut under water and placed in nutrient solution. Shive's "best" three-salt⁵ solution was used at dilutions of 1-100 and 1-1000. Control stems were placed in tap water.

After 24 to 48 hours the salt concentration in the 1-100 solution resulted in burning the leaves severely. The stems continued to survive and produce seed balls when the solution was replaced with tap water.

The stems in 1-1000 nutrient solution continued to grow until the seed and seed balls were mature, and new blossoms were frequently

⁴Indolebutyric acid, 0.1 per cent in lanolin or indolebutyric, 0.4 per cent with para-chlorophenoxyacetic, 0.1 per cent in lanolin.

⁵ KH_2PO_4 0.180 M, Ca $(\text{NO}_3)_2$ 0.052 M, Mg SO_4 0.015 M, with trace amounts of Cu SO_4 , Mn SO_4 , and Fe SO_4 .

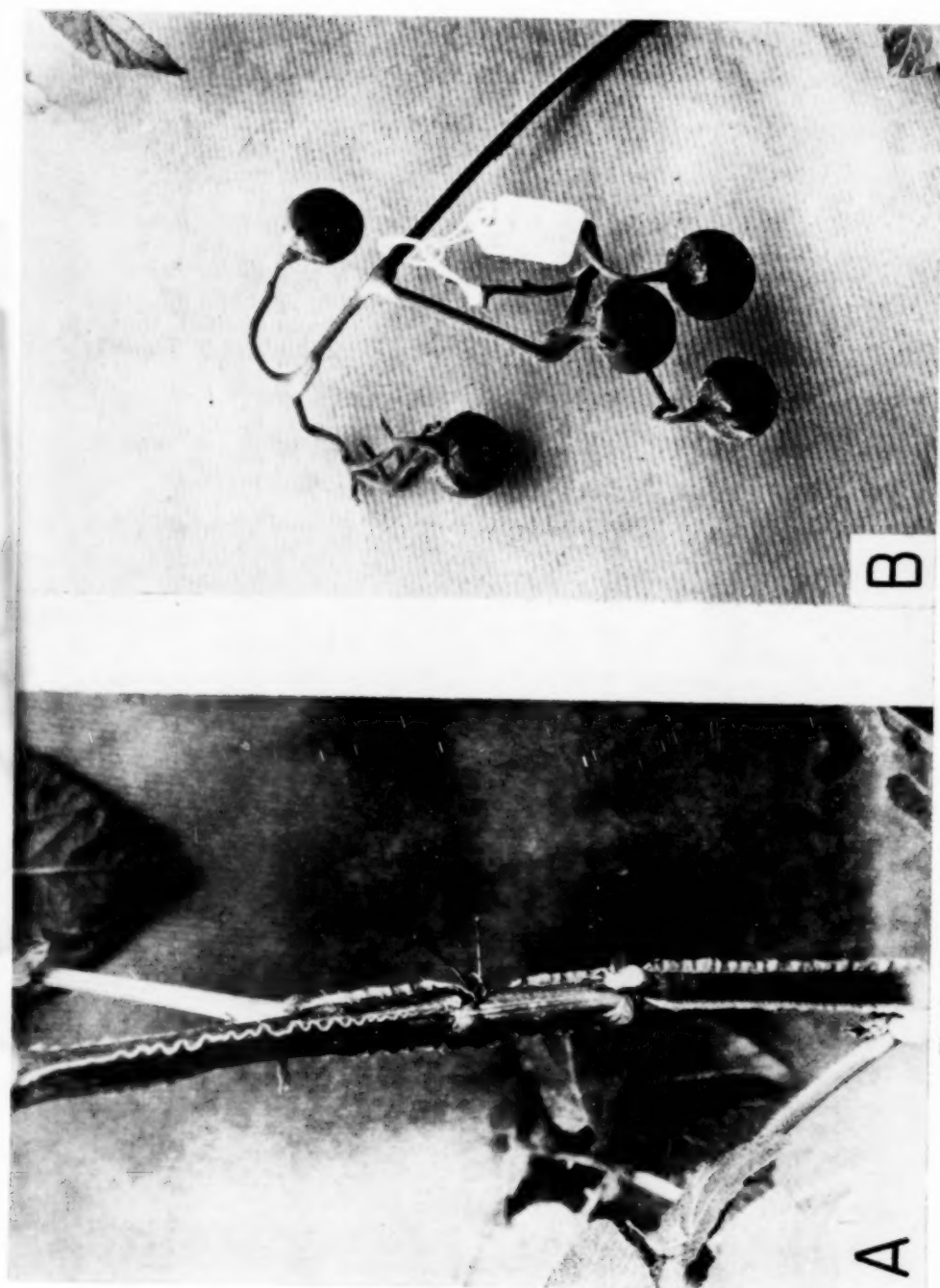


Fig. 1.—A method of obtaining seed on Russet Burbank potato. A. Stem girdled with copper wires. B. Seed balls on girdled stem after fertilization.

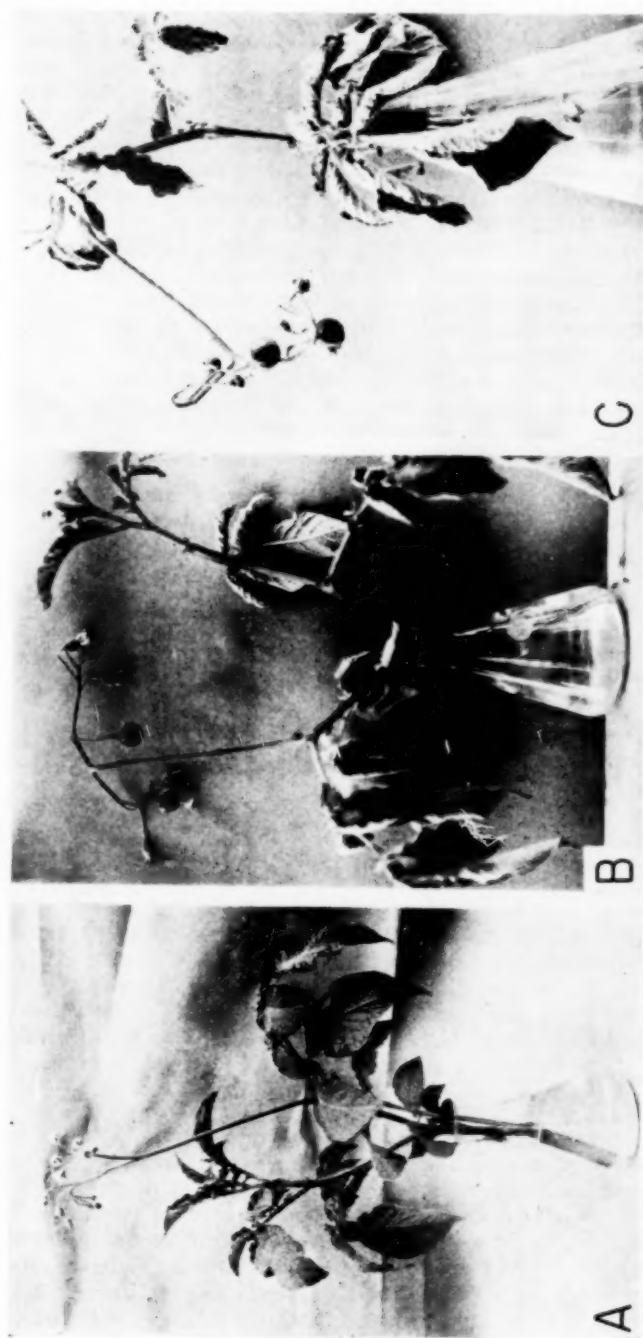


Fig. 2.—A method of obtaining seed on Russet Burbank potato in nutrient culture. A, Flower stalk at time of pollination (1-1000 dilution). B, Flower stalk 18 days after pollination (1-1000 dilution). C, Flower stalk of tap-water control 18 days after pollination.

produced (Figure 2B). Tap water was used to replace the solution lost by transpiration and evaporation; the old solution was replaced by fresh nutrient solution at weekly intervals. The control stems grown in tap water without additional nutrients did not appreciably differ in appearance from those grown in nutrient solution (Figure 2C).

All blossoms were pollinated with pollen from the Menominee variety, when 2 flowers on the cluster were nearly open (Figure 2A). Pollination of very young blossoms had not been previously successful even on girdled plants.

All the blossoms on the Sequoia, Saranac, and B2102-11 varieties produced seed when the stems were grown in nutrient solution. There was an average of 125 seeds per seed ball on these 3 varieties.

Seed balls were developed and maintained on all blossoms of the Russet Burbank variety except the very young ones which were burned by the high concentration of nutrients or the very young ones in tap water. The average numbers of seeds produced by the various methods are shown in table 1.

TABLE 1.—Average numbers of seed balls and seeds produced on stems of Russet Burbank in nutrient culture.

Type of Solution	Average Number of Seed Balls	Average Number of Seeds per Seed Ball
Shive's three-salt solution (1-100):		
Blossoms with flowers open	2.6	123
Very young blossoms	0	0
Shive's three-salt solution (1-1000):		
Blossoms with flowers open	4	125
Very young blossoms	2	115
Tap water:		
Very young blossoms	5	37
Blossoms with flowers open	0	0

Seeds produced on stems grown in nutrient solution or tap water and on girdled plants were tested for germination 4 months after they were harvested. The seed balls were macerated and fermented before the seeds were extracted. The seeds were planted in flats of soil previously disinfected with chloropicrin. No difference due to the method of production was found in the germination of the seed or in the vigor of the seedlings.

DISCUSSION

The production of seed balls on the Russet Burbank variety appears to be correlated with the retention of carbohydrates in the top of the plant, whether by *Rhizoctonia* girdling, by mechanical girdling, or by growing the cut stems in nutrient culture. The leaf symptoms produced by these methods (Figures 2B and C) correspond to those produced where the transport of carbohydrates is restricted, *e. g.*, by leaf roll, *Avenaceum* wilt, or stem damage by *Rhizoctonia*.

The use of growth-regulating chemicals alone has not proved a reliable method for causing seed balls to set on Russet Burbank. It is believed that the excess amount of carbohydrate in the tops of the plants, possibly acts as a stimulus for the production of hormones by the plant which prevent the formation of the abscission layer. Since seed balls are retained and develop even in the absence of pollination, it would appear that favorable conditions for pollination are maintained over a longer period. Darkening of the abscission layer and swelling of the pedicel were noticed as soon as 12 hours after pollen was supplied to the stigma of a flower. These symptoms were generally coincident with the retention of the seed ball and occurred whether or not seeds were formed. It would appear that a combination of growing the stems in nutrient solution plus pollination as early as is feasible would provide the best circumstances for the retention of seed balls by the plant.

The use of nutrient solutions allowed for the pollination of buds younger than had been possible to pollinate on girdled plants. If tissue incompatibility exists between the pollen tube and the stylar tissue in potatoes, this may provide a method of obtaining fertilization by pollination of the young buds.

SUMMARY

Two methods are described for overcoming the difficulty of using Russet Burbank and similar varieties as female parents in potato breeding. The use of a mechanical girdle on the plant or growing cut stems in nutrient solutions has proved satisfactory.

The plant reacts to these treatments by accumulating carbohydrates above the points of constriction or in the cut stem and by retaining and using the seed balls as storage organs. This reaction appears to lengthen the period when successful pollination and fertilization can be accomplished.

POTATO VIRUS X: INOCULATION OF POTATO VARIETIES TOLERANT TO VIRUS Y¹DANIEL A. ROBERTS, F. M. BLODGETT², AND R. E. WILKINSON³

When chronically infected by the common field strains of virus Y (*Marmor epsilon* H.), Placid potatoes (*Solanum tuberosum* L.), if free from other viruses, are practically symptomless carriers. If this variety were increased, it would provide a widespread, easily overlooked source of inoculum. Absence of diagnostic symptoms precludes the practice of roguing as a satisfactory control measure against virus Y in carriers. Infection might not cause serious damage in tolerant varieties, but nearby plantings of less tolerant ones would be endangered, since virus Y is spread rapidly in the field by aphids and causes moderate to severe reactions in most potato varieties.

Virus X (*Annulus dubius* H.) and virus Y in mixed infections cause symptoms that are more than additive in some varieties (15) but not in others (6, 12). If this were true for varieties tolerant to virus Y, then variety-wide inoculations with masked strains of virus X would make possible the use of roguing as a control measure. The successful use of virus X in such a role would depend upon the fulfillment of 4 conditions. The mixed infections should produce diagnostic symptoms, the strain of virus X used should remain masked, and it should neither spread to other plantings nor seriously affect yields.

Variety-wide inoculation with a masked strain of virus X would not be as serious as propagation of plants which carry virus Y. All plants of several common potato varieties apparently are infected by virus X. This virus spreads slowly from field to field because there is no insect vector (9), and masked strains of virus X do not cause drastic yield reductions (2). More severe strains of virus X can be recognized by the symptoms they cause, and their spread can be prevented by roguing. Salaman (26) has demonstrated that tobacco plants already infected by one strain of virus X are protected against infection by another strain in mechanical inoculations.

Experiments were designed to test the practicality of variety-wide inoculation of Placid potatoes with a masked strain of virus X. The effects of single and of dual infections upon symptomatology, yield, respiration, and photosynthesis were studied. Data were taken on the stability of a masked strain of virus X and the field dissemination of this virus.

FIELD TRIALS

Materials and Methods

Stocks of Placid potatoes, tolerant to virus Y, were used in field

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²Deceased.

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tests for 3 years. Some were healthy, whereas others were chronically infected by virus X, by virus Y, or by both viruses. Three strains of virus X, referred to as masked⁴, mild⁵, and severe⁵, were used. In *Datura stramonium* L., these strains caused no symptoms, a mild mottle, and a severe mottle, respectively. The veinbanding strain⁶ of virus Y was used (25). Material was indexed in the greenhouse before it was planted in the field. One seed-piece was taken from each tuber to be tested and was planted in sterilized soil in a 4-in. clay pot. Inoculum from the plants which developed was rubbed on leaves of *Gomphrena globosa* L. and *Physalis floridana* Rydb. to test for the presence of viruses and on *Datura stramonium* to determine the severity of virus X if present. Virus X causes formation of diagnostic local lesions in *G. globosa* (33), and its reaction in *D. stramonium* varies directly with its severity in potato (27). Virus Y causes formation of local lesions in rubbed leaves of *P. floridana* (25).

Seed-pieces from indexed tubers were planted in the field during each of 3 seasons. Each plot consisted of 10 hills, and was replicated 6 times. Plants were rogued which had been improperly indexed, as evidenced by field symptoms. Tubers were harvested and weighed after the first killing frost in autumn. Data were corrected for missing hills, converted to bushels per acre, and analyzed statistically.

Symptomatology

Severe symptoms characterize doubly infected plants of many varieties. However, Bawden and Kassanis (6) and Darby *et al.* (12) reported that when certain potato varieties, already infected by virus X, were inoculated with virus Y, symptoms of current-season infections were no more severe than those caused by virus Y alone. Therefore, it was necessary to determine the severity of symptoms in Placid potatoes infected by a masked strain of virus X and a strain of virus Y which is practically symptomless in this variety. Unless unmistakable symptoms are produced by both of these viruses in Placid potatoes, variety-wide inoculation with virus X would be of no value in diagnosis of plants infected by virus Y.

In the work reported here, chronic infections by both viruses X and Y invariably resulted in diagnostic symptoms of rugose mosaic and leaf-drop streak in Placid potatoes. Symptoms were easily recognizable at all times during the season. Masked virus X in single infections caused no symptoms. Symptoms caused by virus Y alone were detected only during a short period about 6 weeks after planting, when diseased plants were smaller and lighter green than healthy ones. Such symptoms might easily be overlooked during roguing. Plants infected by virus Y recovered rapidly, and were indistinguishable from healthy or X-infected ones by midseason. Roguing does not seem to be a satisfactory control for virus Y in Placid or other tolerant potatoes. However, mixed infections by viruses X and Y in the variety Placid can be readily diagnosed in the

⁴Originally obtained from E. S. Schultz, and maintained by serial transfer in tobacco or Placid potatoes.

⁵Isolated from naturally infected potatoes by W. F. Mai, and subsequently maintained in suitable suspects.

⁶Originally obtained from E. S. Schultz, and maintained by serial transfer in tobacco.

field, even though each virus may be carried symptomlessly in single infections.

Stability of a Masked Strain of Virus X

Salaman (27) concluded that sudden changes of pure strains of virus X in the same plant are rare. He found that no changes occurred after repeated passages through solanaceous susceptibles. Where changes occurred in other plants, all were from a higher to a lower virulence. Clinch (9) reported a progressive reduction in virulence of a severe strain over a 4-year period in potatoes. Bald and White (5) postulated that in mixtures of strains, the severe ones multiply more rapidly than milder ones. Ultimately an equilibrium between strains would be reached, and this equilibrium would vary with different potato varieties. Hutton (17) has shown that passage of a virus X complex through potato seedlings might result in separation of strains.

One possible objection to the use of virus X in variety-wide inoculation of Placid potatoes is that a more severe strain of the virus might be developed over a period of years. Tests were made to determine the stability of the masked strain of virus X used in the experiments reported here.

There was no evidence of increased virulence in the strains of virus X used during a 3-year period. Plants infected by virus X alone were symptomless throughout. More than 50 tubers infected by masked virus X were indexed in the greenhouse after each season. All potted plants and all *Datura* leaves rubbed with inoculum from these plants were symptomless. Inoculum from each plant tested caused the formation of local lesions in rubbed leaves of *G. globosa*, showing that virus X was present. Since it is possible that severe strains of virus X could arise in such infections of Placid potatoes over a period of years, it might be necessary to make periodical inspections of parent stocks to guard against a build-up of more severe strains (5).

Dissemination of Virus X

There is no evidence that insects can transmit virus X in the field, but Walters (31) reported that grasshoppers transmitted the virus from tobacco to tobacco in 6 per cent of greenhouse trials. Clinch (9) concluded that neither aphids nor leafhoppers need be considered as possible vectors of virus X. The virus spreads through contact of sprouts in storage or foliage in the field (9, 19). It is also spread by the cutting knife (7, 18, 20), and there is evidence for its spread by contact of roots (23, 24). Although it seemed reasonable to assume that virus X would not spread rapidly in the field, observations were made during a 3-year period to determine the validity of such an assumption.

No evidence for spread of virus X in field plots was obtained in tests reported here. None of the presumably healthy plants which were indexed in the greenhouse had become infected by virus X, nor did plants infected by virus Y alone become infected by virus X. Severe rugose mosaic and leaf-drop streak were not observed in Y-infected plants in the field, nor was virus X recovered from their progeny in greenhouse indexing tests. It seems unlikely that field spread of virus X would be serious, provided infected and healthy materials were handled separately.

There is already such an abundance of virus X inoculum in nature that inoculation of Placid stocks with this virus would not seriously affect the distribution of virus X.

Influence of Virus Infections upon Yield

Since mixed infections by viruses X and Y in Placid potatoes caused diagnostic symptoms, and since the masked strain of virus X used neither changed into a more severe form nor spread in the field during 3 years, the effect of virus X upon yield would appear to be the most important factor in determining the practicality of using this virus in variety-wide inoculation of Placid potatoes.

Most estimates of yield reductions caused by masked strains of virus X range between 10 and 20 per cent (2, 3, 4, 7, 14, 28, 29). Clinch and McKay (10, 11) were unable to detect any appreciable reduction of yield in Up-to-Date potatoes infected by a masked strain of virus X, and in one instance noted higher yield in diseased than in healthy plots. The presence of virus X might increase the loss caused by other viruses. Mixed infections by leafroll and X viruses caused more drastic yield reductions than were expected on the basis of reductions caused by each virus in single infections (34).

Experiments were designed to determine the influence of infections by virus X, virus Y, and viruses X and Y combined on yields of Placid potatoes. In 1948, lots of healthy and chronically infected tubers were planted in replicated plots at Varna, N. Y. Diseased plants had been infected by a masked strain of virus X, by virus Y, or by both viruses. Plots were planted at Robson Seed Farms, Hall, N. Y. in 1949 and 1950. In 1949, 3 categories of mixed infections were tested, depending upon whether a masked, mild, or severe strain of virus X was used. Two plantings were made, one containing healthy and X-infected plants, the other containing healthy, Y-infected, and XY-infected plants.

Mixed infections resulted in drastic yield reductions, and losses varied directly with severity of the strain of virus X present (Table 1). Infection by virus Y alone caused reductions of about 25 per cent. Reductions caused by virus X alone were not mathematically significant, probably as a result of the small size of the plots. In 1950, X-infected plots produced more than healthy ones. However, the ratio of yields of X-infected to Y-infected was about the same for each of 3 years, an indication that the relatively low yield from healthy plots in 1950 resulted from the influence of some factor or factors affecting only the healthy plots. After samples taken from these plots had been indexed, it was found that about 75 per cent of those plants presumed to have been healthy actually had been infected by virus Y. This offers the most likely explanation for the reduced yield in healthy plots. When virus Y spread in the field to X-infected plots, visible symptoms developed, and doubly-infected plants were rogued.

Although there were no mathematically significant reductions in yield of Placid potatoes caused by virus X alone, the actual yields in 1948 and 1949 are in accord with most reports of masked strains of virus X in other varieties. Since there is no reason for assuming that Placid is affected less by virus X than are other varieties, it appears probable that masked X does cause a slight reduction in yield.

TABLE 1.—Yields per acre of healthy and diseased Placid potatoes.

Class	1948	1949	1950
	Bus.	Bus.	Bus.
Healthy	524	419	513†
Masked X	475	372*	543
Y	353	335	479
Masked X + Y	173	259	287
Mild X + Y	221
Severe X + Y	174
L.S.D., Odds 19:1	59	72	46
L.S.D., Odds 99:1	84	104	67

†75 per cent of plants infected by virus Y during the season.

*Calculated from yields in a separate planting of healthy and X-infected material.

Influence of Virus Infections upon Respiration and Photosynthesis

No reports of measurements of the photosynthetic rates in leaf tissues where virus is carried symptomlessly were found in the literature. It seemed possible that the influence of virus infection upon susceptible photosynthesis and respiration might be a factor concerned in the reduction of yields of potatoes.

There are several reports of increased respiration in virus-infected leaves (8, 13, 32). Other reports indicate that increased respiration does occur, but only during certain stages of the development of the diseased plant. Glasstone (16) compared the respiration of healthy and mosaic-diseased tobacco plants from the time of inoculation until after systemic symptoms had appeared. Respiration of healthy and of diseased plants remained about the same until the time of systemic spread of virus, when there was a sharp increase in the respiratory rates of diseased plants. In chronic infections, there was little or no difference in respiration of healthy and of diseased plants.

MATERIALS AND METHODS

Healthy and diseased Placid potatoes were grown in the greenhouse, and indexed for virus content by inoculation to suitable indicator plants. Leaves of healthy, X-infected, Y-infected, and XY-infected plants were harvested and circular discs with an area of 1 sq. cm. were removed with a Ganong leaf-punch and floated on water. Respiration and photosynthesis in these discs were measured manometrically by techniques described by Umbreit *et al.* (30) and by Muller (21). Four discs were placed in Warburg flasks, with the lower epidermis uppermost. Discs did not overlap. Distilled water was placed in the sidearms to maintain a saturated atmosphere, and in the center wells was placed either a 10 per cent aqueous solution of KOH to absorb carbon dioxide released during

respiration or diethanolamine carbonate buffer (22) to provide an atmosphere containing carbon dioxide (0.4 per cent) for photosynthesis. Flasks were attached to Warburg constant-volume manometers, and allowed to equilibrate for 20 minutes at 30°C. The amounts of oxygen absorbed in respiration or released in photosynthesis were recorded at 15-minute intervals for 2 hours and 1 hour, respectively. Respiration was allowed to proceed in total darkness, and photosynthesis was measured in approximately 1,500 foot-candles illumination supplied by a bank of fluorescent bulbs located below the glass bottom of the constant temperature bath. In all cases, 3 flasks of each category of healthy or diseased tissues were prepared, and the average readings were recorded. Respiratory rates were measured before and after photosynthesis trials. The experiment was repeated twice, and the data treated statistically.

RESULTS

Chronic virus infection did not influence respiratory rates in these tests (Table 2). This agrees with the report (16) that there was no marked difference between respiratory rates in healthy and chronically infected tobacco plants.

It is significant that infection by a masked strain of virus X caused decreased photosynthesis in leaf tissue. Photosynthetic rates were decreased in symptomless Y-infected leaves, and double infections resulted in greatest decrease in rates of photosynthesis.

TABLE 2.—*Oxygen absorbed in respiration and released in photosynthesis by discs of Placid potato leaves in 1 hour at 30°C.*

Kind of Tissue	O ₂ Absorbed*	O ₂ Released†
	μl./cm. ²	μl./cm. ²
Healthy	11.3	62.3
Masked X	11.2	55.8
Y	10.7	52.9
Masked X + Y	11.1	49.6
L.S.D., Odds 19:1	1.7	4.5
L.S.D., Odds 99:1	3.0	6.8

*Test conducted in the dark.

†These figures are corrected for oxygen absorbed during respiration. Illumination of approximately 1,500 foot-candles was used.

DISCUSSION

Control of the disease caused by virus Y in Placid and probably in other carrier varieties would be aided by roguing, provided plants had been infected previously by virus X. Symptoms from mixed infections are diagnostic, even when a masked strain of virus X is present, whereas those from single infections by virus Y in such varieties are practically

masked. There seems to be little danger of field spread of virus X, and there is no good evidence that a masked strain of this virus will undergo rapid and variety-wide conversion into a severe strain. There exists the possibility of a gradual change over a long period, but there is no evidence that such may occur. Changes within individual plants would be detected in roguing, and such plants would be eliminated.

The advisability of using virus X in inoculations as suggested here depends upon its influence upon the cropping power of potatoes. It seems likely that the effect of a masked strain on yield is too serious to warrant its use in inoculation of Placid potatoes, where the desirable features might not outweigh the disadvantage of yield reduction caused by virus X. If a variety of potato is developed which has exceptionally outstanding agronomic or disease resistance characteristics, but which is a carrier of virus Y, artificial infection by a masked strain of virus X as proposed here might be profitable.

Systemic infections by viruses which invade leaf parenchyma apparently result in a decrease in the rate of photosynthesis, regardless of the symptoms produced. The reductions in yield caused by masked strains of virus X can be attributed, at least in part, to reduced photosynthesis in diseased plants. The effects upon photosynthesis of the several chronic infections closely parallel those upon yields.

It would appear that photosynthesis might become limiting for growth and tuber formation in diseased plants under certain field conditions, even in the absence of visible symptoms. This is supported by the suggestion made by Bald (1) that in winter, when virus X most severely affected the growth of *Datura* plants, photosynthesis and gaseous exchange are likely to be limiting in greenhouses.

Bald (3) attributed the effect of a masked strain of virus X upon the yield of Up-to-Date potatoes to the inability of diseased plants to transport hydrolyzable reserve leaf proteins to the tubers for late-season expansion. There was no difference between the yields of healthy and X-infected plants which were harvested 14 to 15 weeks after emergence of the plants, but at maturity, diseased plants yielded about 11 per cent less than healthy ones. It was suggested that final rapid tuber expansion at maturity was due to the translocation of reserve proteins from senescent leaves in normal plants, and that virus infection interfered with the emptying of such reserves from diseased leaves. However, in view of the decreased rates of photosynthesis in virus-infected tissues, regardless of severity of symptoms, an earlier suggestion (1) appears to provide a more logical explanation for the reduced yields of potatoes infected by a masked virus. Decreased photosynthesis in diseased plants probably makes less carbohydrate available to tubers during the phase of most rapid expansion.

SUMMARY

Placid potatoes carry virus Y symptomlessly except for a short period about 6 weeks following planting. The inoculation of Placid stocks with a masked strain of virus X would make possible the control of virus Y by roguing since mixed infections by these viruses cause rugose mosaic and leafdrop streak.

No evidence was obtained indicating that the use of a masked strain

of virus X in such inoculations would endanger other potato varieties. In a 3-year period, there was no spread of the virus from diseased lots to separately-handled healthy lots. During the same period, there was no evidence of conversion of the masked strain into a more severe one.

Infections by virus Y and by both viruses X and Y combined caused yield reductions of approximately 25 and 50 per cent, respectively. Virus X did not cause statistically significant yield reductions, but X-infected plots tended to yield less than healthy ones. Because of the possibility that a masked strain of virus X might reduce yields, it does not seem advisable to recommend its use in inoculation of symptomless carriers of virus Y unless such a variety were developed which has outstanding agronomic or other desirable characteristics.

Chronic infections by viruses X, Y, or by both viruses did not influence respiratory rates in Placid potato leaf discs, but did reduce the rates of photosynthesis. This probably accounts for at least part of the yield reductions caused by infections with these viruses.

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APHID (HOMOPTERA: APHIDIDAE) INFESTATIONS ON CHIPPEWA, KATAHDIN, AND THE NEWLY RELEASED BLIGHT-RESISTANT VARIETIES CANSO AND KESWICK¹R. H. E. BRADLEY, R. Y. GANONG AND D. W. RIDEOUT²

INTRODUCTION

When the blight-resistant varieties Canso and Keswick are grown, the need for fungicidal control is reduced but the need of insecticidal control remains (1,2). During the past 10 years, much emphasis has been placed on the control of aphids on potatoes in Eastern Canada. A field experiment was conducted in 1951 to determine what aphid infestations growers might expect on the newly released blight-resistant varieties Canso and Keswick.

EXPERIMENTAL DESIGN AND METHODS

The aphid infestations that developed on Canso and Keswick were compared with those that developed on the established varieties Chippewa and Katahdin.* Tubers of Canso and Keswick were supplied by Mr. L. C. Young, Canada Experimental Station, Fredericton, New Brunswick; and foundation tubers of Chippewa and Katahdin were used. The experiment was conducted at the Field Crop Insect Field Station, near Fredericton. The land had not been cultivated for more than 20 years, and the time required to prepare the ground delayed planting until June 12. The experimental plan was a 4 x 4 latin square; plots were 35 feet square (12 rows of potatoes in each), and separated from one another by 15 feet of fallow ground. Drills were made by machine, fertilizer (Albatross granular 5-10-13-1) being applied at the same time at about 2000 pounds per acre. The tubers were cut and planted by hand, and the potatoes were cared for as if grown commercially except that no insecticides were applied to control aphids. Each week, the plots were sprayed with a mixture of a copper fungicide and calcium arsenate to control blight and biting insects (although Canso and Keswick did not require fungicidal control, the same spray was applied to all the plots).

Aphid counts were made every 10 days from July 25 to September 20. Counts were made on an upper, a middle, and a lower leaf from each of 10 plants selected from the middle four rows of each plot. Aphids were identified to species and recorded as alatae (winged), adult apterae (wingless adults), and nymphs. The numbers of upper, middle, and lower

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*Under similar conditions in the field, the spread of potato leaf roll is less in Katahdin than in Chippewa (5,6). As a secondary study, the spread of leaf roll in plots of Katahdin and Chippewa was followed and compared with the aphid infestations. The results of this part of the experiment will not be known until 1952.

leaves on 20 plants of each variety were counted on August 16, and the numbers on 10 plants of each variety on August 31. As there were no significant differences in the numbers of upper, middle, and lower leaves per plant on August 16 and 31, the numbers of leaves on 30 plants of each variety were averaged and the results used as the mean numbers of leaves per plant for all counts. With these data, the numbers of aphids per plant were calculated as in previous experiments (3,4).

RESULTS AND DISCUSSION

Plants of all four varieties appeared above ground during the first week of July. Two nymphs of *Myzus persicae* (Sulz.) were found on July 8, when more than 100 leaves were inspected for aphids. Aphids were observed on all plots, with the exception of three, on July 18, when the first regular aphid count was made. On the 480 leaves examined at this time (30 from each plot), 17 aphids were found: two were of *M. persicae* (one winged, one adult aptera), ten were of *Macrosiphum solanifolii* (Ashm.) (one winged, seven adult apterae, two nymphs), and five were of *Aphis abbreviata* Patch (one winged, three adult apterae, one nymph). The presence of adult apterae of all three species on July 18 indicates that the potatoes were probably infested by winged aphids before July 8, i.e., soon after emergence.

The mean numbers of aphids per plant on each of the four varieties for each date of counting are given in figure 1. Figure 1 shows that the numbers of aphids per plant on Canso, Keswick, Chippewa, and Katahdin were similar throughout the season; differences between varieties were small and not consistent. During July, more than 70 per cent of the aphids found were of *M. solanifolii*, and this species continued to be the most numerous until the middle of August. Table 1 shows the percentage of the total aphid population for each species between August 13 and September 20. During this time, more than 60 per cent of the aphid population were *M. persicae*. Table 1 also shows that the aphid infestations on each of the varieties were similar for each species. Further-

TABLE 1.—Percentage of total aphid population for each species on four varieties of potato at Fredericton, New Brunswick, 1951.

Date	Chippewa			Katahdin			Canso			Keswick		
	<i>M.p.</i>	<i>M.s.</i>	<i>A.a.*</i>	<i>M.p.</i>	<i>M.s.</i>	<i>A.a.</i>	<i>M.p.</i>	<i>M.s.</i>	<i>A.a.</i>	<i>M.p.</i>	<i>M.s.</i>	<i>A.a.</i>
Aug. 13	61	31	8	55	41	4	48	48	4	22	31	47
Aug. 24	62	11	27	85	8	7	87	7	6	77	12	11
Aug. 31	76	13	11	86	3	11	87	2	11	59	6	35
Sept. 12	62	4	34	78	9	13	82	3	15	69	8	23
Sept. 20	75	15	10	—	—	—	85	1	14	64	6	30

**M.p.*=*Myzus persicae* (Sulz.), the green peach aphid.

M.s.=*Macrosiphum solanifolii* (Ashm.), the potato aphid.

A.a.=*Aphis abbreviata* Patch, the buckthorn aphid.

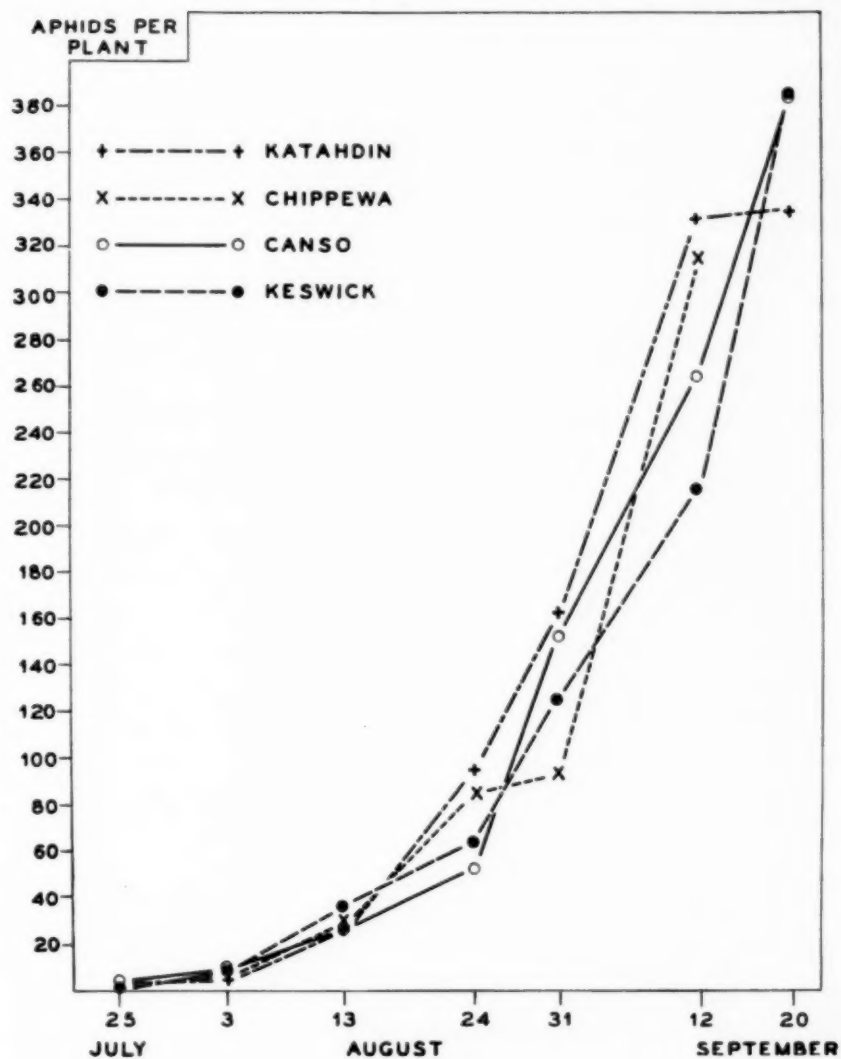


Fig. 1.—Mean number of aphids per plant on each of four varieties of potato for each date of counting at Fredericton, New Brunswick, 1951.

more, the numbers of winged, adult apterae, and nymphs found on each of the varieties were similar. The number of winged aphids was usually less than one and never exceeded three per plant. Throughout the season, from two to four times as many nymphs as adult apterae were found.

These results show that similar aphid infestations developed on Canso, Keswick, Chippewa, and Katahdin when grown in the field under similar conditions in 1951. On the basis of these results, aphid control practices that have been used successfully on Chippewa or Katahdin should also be applied to Canso and Keswick.

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REDUCING SUGAR CONTENT OF MAINE-GROWN POTATOES
TREATED WITH MALEIC HYDRAZIDE¹M. E. HIGHLANDS, J. J. LICCIARDELLO AND C. E. CUNNINGHAM²

Accumulation of reducing sugars in white potatoes during storage at low temperatures has for some time been a problem to processors, especially in the field of potato chips and dehydrated potatoes. This problem has acquired additional significance in the production of canned whole white potatoes as well as frozen french fried potatoes where an undesirable brown or deep tan color is objectionable in the finished product.

Ross (3) has shown that reducing sugars in Katahdin varieties stored at 40°F. for 150 days increased from an initial 1.4 per cent to 5.7 per cent. Green Mountain tubers under the same storage conditions showed an increase from an initial content of 3.8 per cent to 6.3 per cent.

Methods for alleviating this condition have been suggested by many, the main approach being to store the potatoes at temperatures of 50°F. or above after digging. Another procedure has been to store the potatoes, after withdrawing from cold storage, at elevated temperatures for varying lengths of time to permit the accumulated sugars to dissipate before using for processing.

Recently Wittwer (5) has suggested that less reducing sugars accumulate during cool storage when the growing potato plant has been treated prior to harvest with maleic hydrazide at levels of 1000 ppm and 2500 ppm.

Patterson *et al* (1) have indicated that Cobblers and Pontiacs treated with foliar sprays of maleic hydrazide, at corresponding levels six weeks prior to harvest and stored for seven months at 45°F. show an appreciable reduction in the accumulation of reducing sugars when compared with untreated controls. Furthermore, potato chips produced from potatoes so treated are reported to be superior in color to those prepared from untreated stock.

MATERIALS AND METHODS

Kennebec and Katahdin varieties of potatoes were grown on Caribou loam Aroostook soils during the 1951 season.

Foliar spraying with maleic hydrazide was carried out on test plots for each variety at intervals of 37, 27, and 20 days prior to harvest. Sprays were applied at the rate of 150 gallons per acre at levels of 2500 ppm and 1000 ppm. Control plots received the same treatment as treated plots except that no maleic hydrazide was used.

Following digging the harvested lots were stored at 40°F. for six months.

The various lots of tubers were then withdrawn from storage and analyzed for reducing sugars. Colorimetric methods of analyses were employed as described by Pol and Edson (2) with modifications as recommended by Ross *et al* (4). A composite sample of five tubers approximately two inches in diameter was taken for each determination.

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TABLE 1.—*Reducing sugar content of Maine grown potatoes treated with maleic hydrazide and stored for six months at 40°F.*

Sample	Days Prior to Harvest of Application	Per cent Concentration Applied	Gallons/Acre Rate of Application	Per cent Moisture in Sample	Mg/cc Reducing Sugar in Potato Juice	Per cent Reducing Sugar, Moisture-Free Basis
1-A Katahdin	37	0.25	150	78.7	22.2	8.2
2-A Katahdin	27	0.25	150	78.9	19.7	7.4
3-A Katahdin	20	0.25	150	80.8	19.7	8.3
4-A Katahdin	0	0.00	0	81.3	18.9	8.2
1-B Katahdin	37	0.10	150	79.8	19.6	7.8
2-B Katahdin	27	0.10	150	78.8	18.0	6.7
3-B Katahdin	20	0.10	150	79.3	18.7	7.2
4-B Katahdin	0	0.00	0	79.1	19.2	7.3
1-A Kennebec	37	0.25	150	79.5	11.0	4.3
2-A Kennebec	27	0.25	150	80.5	10.3	4.3
3-A Kennebec	20	0.25	150	82.5	11.3	5.1
4-A Kennebec	0	0.00	0	79.0	9.7	3.7
1-B Kennebec	37	0.10	150	79.1	10.4	3.9
2-B Kennebec	27	0.10	150	79.3	11.0	4.2
3-B Kennebec	20	0.10	150	80.2	8.6	3.5
4-B Kennebec	0	0.00	0	79.0	10.6	4.0

The tubers were washed under a stream of cold water and the excess moisture was thoroughly dried from the surface of the tubers. The potatoes were cut into small segments, comminuted in a Waring type blender for five minutes, the juice squeezed through gauze cloth and centrifuged for ten minutes at 3600 rpm. Analyses were conducted on this centrifuged juice in triplicate. Total solids were determined according to the vacuum oven method of the Association of Official Agricultural Chemists (6).

Potato chips were prepared from each sample lot. The chips were fried in triple X Vream at a temperature of 375° for 3 minutes.

RESULTS

Results of analyses for reducing sugars are shown in table 1.

Potato chips prepared from like samples were examined for variation and intensity of color.

Those chips prepared from Kennebecs were light in color but no appreciable color differences between controls and treated stock were apparent. Chips prepared from Katahdins were very dark. There was no appreciable difference between controls and untreated samples.

SUMMARY AND CONCLUSIONS

Potatoes of Kennebec and Katahdin varieties when treated with maleic hydrazide under conditions noted above show no significant reduction in accumulation of reducing sugars compared with untreated controls when stored at 40°F. for six months.

Appearance and color of potato chips prepared from like samples show no significant differences within the variety.

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